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Breeding behavior of captive emperor penguins (Aptenodytes forsteri) : a thesis ...

Mary Elizabeth Kiel
University of the Pacific

BREEDING BEHAVIOR OF CAPTIVE EMPEROR PENGUINS (APTENODYTES FORSTERI)

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Mary Elizabeth Kiel

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Mary Elizabeth Kiel

is approved for recommendation to the Committee on Graduate Studies, University of the Pacific.

Department Chairman or Dean:

Thesis Committee:

Chairman

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Abstract

Breeding behavior of captive Emperor Penguins (Aptenodytes forsteri) was observed at Sea World, San Diego, California during July, August, and September 1980, and April 1981. Emphasis was on displays, courtship, egg-laying, incubation, and care of chicks.

I observed the trumpet display most often between birds of opposite sexes and I interpret it as a signal of sexual identity. I interpreted the sideways stare display as a signal of sexual identity important in pair bond maintenance. Three head movements studied shared several functions including comfort behavior and reduction of intraspecific aggression. My observations confirmed that the display walk occurs in Emperors and is used by males to attract females. The single note cry allows separated members of a pair to find each other.

Results of an attempt to sex Emperor Penguins by vocalization are reported.

Introduction

This is a study of the courtship and incubation behavior of captive Emperor Penguins conducted at Sea World, San Diego, California in July, August, and September 1980, and April 1981.

Penguins are among the most primitive living birds (Peterson, 1973). They appear to have evolved in the southern hemisphere, since all penguin fossils are found within the range of the present day species (Simpson, 1975). There are 17 extant species inhabiting southern hemisphere seacoasts (Peterson, 1973).

While the Galapagos Penguin (Sphenicus mendiculus) lives as far north as the equator, other species live farther south (Peterson, 1973). Emperor Penguins are circumpolar. They breed on the sea ice of the Antarctic continent and islands between 66°S and 77°S latitude (Murphy, 1936). Twenty-four Emperor breeding colonies are known, with an estimated world population of 240,000 breeding birds (Stonehouse, 1975).

In these latitudes the Emperors have few predators on land; giant petrels (Macronectes giganteus) and skuas (Stercorarius skua) can take unguarded chicks or eggs (Spellerberg, 1975). Adult Emperors fall prey to leopard seals (Hydrurga leptonyx) and killer whales (Orcinus orca) (Spellerberg, 1975).

The Emperor is the largest extant species of penguin. Its mean weight is 30 kg and its mean length is 115 cm (Stonehouse, 1975). It has a lesser surface volume to mass ratio than smaller penguins and loses proportionally less heat (LeMaho, 1977). Emperors also have smaller feet, bills, and flippers, in proportion to their size than do other penguins (Peterson, 1973). Another thermoregulatory factor is behavioral; Emperors hold their eggs on their feet and huddle together to conserve heat and energy (LeMaho, 1977). These adaptations allow Emperors to breed during the harsh Antarctic winter.

The only other penguin breeding in Antarctic latitudes is the Adelie (Pygoscelis adeliae) (Simpson, 1976). Adelies reach their breeding grounds in early October, lay their eggs by the end of October, and the eggs hatch in mid-December (Murphy, 1936). Average incubation time is 32-38 days (Reid, 1965). Because of their small size, Adelies are able to raise their chicks by the end of the Antarctic summer (Peterson, 1973). The larger Emperors need more time to raise their chicks to independence and have evolved a completely different breeding schedule (LeMaho, 1977).

After arriving in the rookeries in March and April, the birds court, pair, and begin copulating (Mougin, 1966). The female lays a single egg in late May or June and passes it to her mate, who incubates it on his feet, covered with a patch of skin called the brood patch, for most or all of the 62-64 day incubation period (Yeates, 1975). The male fasts during this time and may lose up to 50% of its body weight (Prevost, 1961). Females go to sea to feed, returning at the end of the incubation period in July or August (Peterson, 1973). They relieve the male of the egg or newly hatched chick. The males then feed at sea while the females incubate and feed the chicks. When the chicks are approximately one month old, both parents go to sea and return to feed the chicks. This continues until the chicks molt and go to sea in December or January. The adults then molt and return to sea (Yeates, 1975).

There have been several studies of Emperors in the wild (Prevost, 1961; Mougin, 1966; Isenmann, 1971; Stonehouse, 1975; Yeates, 1975). However, Scheich's (1980) work on vocalizations is the only previous study of captive Emperors.

Methods and Materials

My study subjects were 45 Emperor Penguins at the Antarctic Penguin Research Facility, Sea World-Hubbs Research Institute, San Diego, California. These birds were collected in November of 1976 and 1977 at McMurdo Sound, Antarctica (Todd, 1980). They were assumed to be subadults at the time of collection since breeding birds were not taken. Most of the birds were marked with numbered bands placed around the base of the flipper.

The unit in which the birds were housed contained the following penguin species: Emperors (Aptenodytes forsteri) 45; Kings (Aptenodytes patagonica) 15; Rockhoppers (Eudyptes crestatus) 3; Macaronis (Eudyptes chrysolophus) 3; Gentoo (Pygoscelis papua) 1; Adelies (Pygoscelis adeliae) 132. The unit consisted of a 26m X 11m enclosed freezer with three observation windows. It contained two salt water pools (5m X 4m X 1.5m deep and 4m X 2.5m X 1.5m deep) filled with water filtered from adjacent Mission Bay. Air temperature was maintained at -8^{o}C to 3^{o}C and the floor was covered with ice. An austral lighting schedule was followed in the unit (Todd, 1980), although it was not strictly adhered to during my study. (Lights were turned up to allow staff members to work and to facilitate photography and observations.)

The Emperors were fed a diet of thawed frozen herring (Clupea harengus) supplemented with Sea Tabs (vitamins), cod liver oil, and dicalcium phosphate tablets (Todd, 1980). The birds were fed by hand, by throwing fish in the pool and from troughs inside the unit.

I made most of my observations inside the freezer, although some were made through the observation windows to minimize disturbance.

After an egg was found in one of the pools, all pairs with eggs were placed in a plywood enclosure within the unit, preventing them from going in the pools while holding an egg. Mates of incubating birds were allowed to leave and return to the enclosure. Fish were

placed in the enclosure for incubating birds and attempts were made to feed birds that had lost a conspicuous amount of weight.

I observed courtship and incubation activities for a total of 107 hours distributed over 27 days in July and August, 1980. I concentrated observations between 0700 and 1300 hours, when the birds were most active. During observations of special interest, such as egg-laying, I continued observations until the unit was closed at 1700 or 1800 hours. Studies of chicks and their parents took place from 22 September to 26 September 1980 in 8 hour shifts (continued by the staff on a 24 hour basis). During this time a television monitor was used.

Although I was unable to observe all of the birds simultaneously, I made notes of the following displays as I observed them: the trumpet display, the sideways stare, the head nod, the head shake, the head twist, the display walk, and the single note cry. I also recorded any birds that were seen standing together as a pair.

In order to determine sex, Ann Bowles and I recorded vocalizations during March and April 1981. Tape-recorded Emperor chick vocalizations were used to elicit responses from captive birds. Ann Bowles judged the sex of each bird according to its vocalization and I wrote them down.

Results

Huddles and Trios

Huddles were observed each day (18 times) during July in the early morning. The Emperors stood together with bodies touching and necks relaxed so that their bills rested on their chests. The huddle formed between the wall and the pool and broke up as staff members entered the unit at 0700 hours. It did not re-form during the day. Incubating birds placed together in an enclosure did not huddle; although they stood close together they were rarely close enough to touch a bird other than their mates.

I observed trios daily at Sea World during June, but made no written records of them. The birds stood in groups of three, beating each other with their flippers. By July, when I began recording behavior, trios were no longer forming.

Copulation

I observed 6 copulation attempts on 30 June, 1 July, and 11 July. All attempts were by pairs that later produced eggs. I defined an attempt as a male placing his bill on a female's neck and pressing her down.

On 30 June, bird #27Y attempted to copulate with #4G by placing his beak over her neck and pressing her down on the ice. He did this unsuccessfully three times, lunging and twisting his head at passing birds between each attempt. Afterwards he preened for three minutes.

On 1 July, birds #3Y and #11Y attempted to copulate in the manner previously described. The male climbed on the female's back, then another pair approached them. When the approaching pair was about two feet away, the copulating pair got up, nodding their heads. The male preened for less than a minute, then placed his beak over the female's neck. The second pair approached again and the copulating pair

stopped, nodding their heads and lunging at the approaching pair.

Approximately three hours later #3Y placed his beak over his mate's neck. Another nearby pair also attempted to copulate, the male pressing down on the female's neck twice. The pair that had approached #3Y and #11Y earlier in the day also attempted to copulate.

On 11 July, copulation was attempted by a pair which was found holding an egg 2½ hours later. After the attempt the female showed her brood patch by lifting the fold of skin that usually hides it.

Egg-laying

In Antarctica most eggs are laid in May or June (Prevost, 1961). The captive birds laid their eggs later: on 11 July, 12 July, 17 July, and 28 July. These eggs were all found before noon (Table 1).

I observed one female actually laying an egg. At 1046 hours on 17 July, I observed birds #3Y and #11Y standing together, swinging their heads and pecking at any birds that came near. The female (#11Y) appeared to have three contractions within two minutes before the egg was laid at 1103 hours. Her mate was standing directly behind her. The pointed end of the egg appeared first and the female immediately placed the egg on her feet. She then bent over several times, lifting her brood patch and touching the egg with her bill. The male walked around her, faced her, and bent over and touched the egg.

Egg Exchanges

I observed three egg exchanges (Table 1). In the first, the egg was discovered by a staff member at 1154 hours. The female put the egg on the ice eight times, trumpeting to the male each time, and pushed the egg back onto her feet with her bill before the male had a chance to take it. She turned around frequently while holding the egg,

the male following her. The staff felt that the egg was being chilled from being left on the ice so often, so the egg was taken and a dummy egg was offered to the female. She accepted the dummy egg and the real egg was placed in an incubator at 1745 hours, six hours after it was first seen. It proved to be infertile. The female kept the dummy egg for approximately 78 hours, then gave it to the male. This exchange was not observed.

In another case an egg was found by a staff member at 1840 hours, in the possession of the female. She lifted her brood patch 20 times an hour for the next three hours, and touched or pointed to the egg frequently. The male also pointed to the egg. The male stayed next to the female, preening himself twice for three minutes each time during the three hours. At 1151 hours the male trumpeted and moved closer to the female. They continued pointing at the egg until 1303 hours, when the female stepped back, leaving the egg on the ice. The male immediately rolled the egg onto his feet, using his bill. The female trumpeted and the male began showing the egg. They continued to trumpet and point to the egg for the next hour. Then the female started to walk around the unit, followed at a slower pace by the male, which was hampered by the egg. At 1729 hours, when my observations ended, the pair was still trumpeting and standing together. The next morning the female was standing next to the pool. The male was in the pool and the egg was found at the bottom of the pool. A dummy egg was presented to the pair. They pointed at it but did not take it. The dummy egg was then removed from the unit.

The third exchange was observed for approximately 1½ hours on a videotape made by a staff member. The female had the egg and showed it to the male fourteen times. During this time the male's interest in the egg appeared to increase, as he began touching the egg with his beak more and more frequently. He was irritable, pecking at other

birds when they came near. After about 1½ hours, the male took the egg as the female stepped back to leave it on the ice. The male then touched the egg several times and the female lifted her empty brood patch four times.

Incubation

The egg is incubated on the feet and covered by the brood patch. The length of incubation of the four pairs studied that hatched eggs was 66 days for three of the pairs, and 58 days for the last pair (mean = 64 ± 4 days). The fith pair, which accepted a dummy egg, incubated it for 61-68 days (exact number not known), then abandoned it. The male of the sixth pair abandoned the egg within the first 24 hours and did not accept a dummy egg.

Incubating birds had a low level of activity, rarely moving except to follow their mates around the enclosure. The only movements seen in incubating birds were comfort movements such as yawning, stretching, preening, and aggressive lunges at birds standing close by.

The birds generally stood close together, rarely touching, and always stood by their mates if their mates were in the enclosure.

Non-breeding Emperors also showed an interest in incubating. I observed five non-breeding birds incubating chunks of ice the same size or slightly larger than Emperor eggs.

Chicks

Emperor chicks are fed by regurgitation. In a typical feeding, the chick, held on its parent's feet, began vocalizing and the parent responded by lifting its brood patch and bending over to touch the chick. The adult raised its head, regurgitated, and, holding the contents in its mouth, bent over so that the chick could feed from its open beak. I also observed non-breeding birds regurgitating in July

and August. They usually regurgitated on a large chunk of ice rather than the smooth ice that covered most of the floor of the unit.

In the wild, chicks usually begin hatching in July, although the date may vary with the latitude (Mougin, 1966). The Sea World chicks hatched in early September. After the chicks hatch, the parents and their neighbors may become very aggressive, with "rugby matches" occurring for possession of the chicks. This phenomenon was observed at Sea World during the 1979 breeding season over an egg. It was described as a scrimmage by Todd (1980).

Pair Bonding

The seasonal pair bond is strong in captive Emperors. While most Emperors stand alone or in loose groups when not huddling together for warmth, paired Emperors were observed standing next to each other (touching or close enough to touch) and slightly apart from the other birds. During the month of July the six pairs that had eggs were observed standing together as a pair 20.0 ± 9.2 times. Birds that did not lay eggs were observed standing together in pairs only 4.7 ± 7.7 times.

The captive Emperors stayed with their mates throughout the season. Separating paired birds (that later produced eggs) by stepping between them resulted in attempts to return to the mate. The separated birds stretched their necks to full height, tried to keep the mate in visual contact, and uttered a loud squawk (the single note cry). Even after the eggs were laid, the birds always returned to their own mates after feeding outside the enclosure, and remained standing next to their mates. The paired birds expressed no interest in birds other than their mates. Each member of a breeding pair displayed only to its mate and did not respond when other Emperors displayed to it. The only exception was the male whose egg was found in the pool. This bird responded to

another Emperor's display after the egg was lost, but it also displayed to its mate. By contrast, non-breeding birds were seen with from 1 to 13 other birds (mean = 3.1 ± 1.9).

Trumpet Display

The courtship song or trumpet display described by Stonehouse (1953), Prevost (1961), and Scheich (1980), is performed as a duet with another Emperor, by the bird alone or by the bird to an inanimate object.

In the trumpet display, the bird drops its beak to its chest, raising the brood patch. The bird leans forward and begins the song, during which the head is raised and the patch covered (Figure 1). The bird may then twist its beak in an arc over the shoulder (the head twist), nod its head up and down, or perform the sideways stare display.

When the display is performed as a duet the two birds stand side by side, facing slightly inward so that they are at approximately right angles from each other, close enough so that they touch or almost touch. The first bird drops its head, and if the second bird also drops its head, the first bird begins the song, the second bird starting a second or two later. The trumpet is also performed by Emperors to Adelie Penguins in the unit.

The trumpet display occurred throughout the observation period, but greatly increased among non-breeding birds when the eggs were laid. It was never observed between paired birds before the eggs were laid, but was performed frequently during egg exchanges.

In March and April 1981, Ann Bowles and I sexed the birds according to their trumpet vocalizations. A tape of chick vocalizations was played, eliciting a large number of trumpet displays. Twenty-two non-breeding birds, 12 paired adults, and one chick were sexed by this method. In five of the six pairs the sexing by vocalization agreed with the observed sexual roles during the breeding cycle. The sexes assigned

to the sixth pair did not agree with my previous observations. The bird that had performed most of the incubation duties was assumed to be the male, but sexing by vocalization implied that it may have been the female. Neither copulation nor egg-laying were observed to confirm the sexes of the birds (Table 2).

With the sexes of 22 non-breeding birds tentatively established by vocalization, I was able to determine that the trumpet display was initiated by females 57 times and by males 26 times. It occurred between members of the opposite sex 41 times, between males 7 times, and between females 3 times (Table 3).

Sideways Stare Display

In the sideways stare, called "face-to-face" by Prevost (1961), two birds stand side by side, close enough to touch, point their beaks up, stretch to full height, lean apart, and stand motionless (Figure 2).

Among captive birds this display was most frequently observed by itself or after a trumpet display between two non-breeding birds. I observed it 31 times by itself (not in conjunction with another display), 29 times after a trumpet display, 6 times before a trumpet display, once after a copulation attempt, and once before and after a display walk. In non-breeding birds sexed by vocalization, this display occurred 12 times between members of the opposite sex, 3 times between females and never between males (Tables 3 and 4).

Like the trumpet display, I did not observe the sideways stare between breeding pairs before the eggs were laid. It was not observed during egg exchanges or incubation, although the trumpet display was.

Head Movements

I noted three head movements. In the head shake, the head is moved from side to side. I observed this movement after I had separated two

birds of a pair, after a bird ate ice, after lifting the brood patch to show a chick, and after trumpet and sideways stare displays. It was seen most often in conjunction with comfort behavior.

The most frequently noted head movement was the nod, the head moving rapidly up and down several times. This was seen during any disturbance, such as another bird approaching too closely, or when a pair was separated. It appeared often during egg exchanges, after beginning a trumpet display that was not completed, and before and after the sideways stare. I also observed head nods after a bird lifted its brood patch to show a chick.

The third movement is the twist, in which the head is moved in a loop over the shoulder. I saw this movemet in several contexts. During copulation attempts, egg exchanges, or while showing the chick, it was directed toward any bird that came close (except the mate). The head twist also appeared after the trumpet display, but was not directed toward another bird (Table 5).

Display Walk

I observed the display walk twice. Once I saw it performed by a bird which was not followed (the sex of the bird was unknown). The second time it was preceded by a mutual sideways stare, then the male began the display walk, followed by the female (walking normally). Afterwards they engaged in another sideways stare.

Single Note Cry

This loud squawk was heard in three instances among the captive birds: when I separated a pair by walking between them; when one bird of a pair with an egg was outside the mate's enclosure; and when a tape of chick vocalizations was played to a non-breeding male.

Discussion

Huddles and Trios

In the wild, huddles are an important way to maintain body heat and thus conserve energy. Prevost (1961) noted that birds in a huddle lost weight half as fast as individual birds.

Huddles occur nocturnally during pair formation and constantly during incubation, especially in bad weather (Prevost, 1953). Mougin (1966) stated that incubating and non-incubating birds form separate huddles.

The Sea World birds did not huddle as much as birds in the wild, probably because the temperature wasn't nearly as low as it would have been in Antarctica.

Although Emperors are monogamous during any one breeding cycle, there is a time when trios are formed. These appear in March, are most numerous in early to mid-April, and usually disband by the end of April (Mougin, 1966). I observed trios in June. Three birds stood together, beating each other with their wings, Isenmann (1971) and Jouventin (1975) stated that trios consist of a male and two females. Mougin (1966) maintained that trios are experienced adults with juveniles. Data on captive birds are insufficient to support either view.

Copulation

The copulation attempts observed were late in the cycle, occurring in July rather than April as they do in the wild (LeMaho, 1977). Mougin (1966) observed copulations in the wild from 10 April to 10 June. The lateness of the captive birds may have been due to the fact that the austral lighting schedule was not carefully maintained.

Prevost (1961) noted that the first step in copulation is the male placing his beak over the female's neck. He also noted that copulating couples are the target for attacks by other birds. While none of the

pairs I observed was attacked, one was approached twice by another pair, and both times the copulation attempt was terminated.

Egg-laying

Yeates (1975) observed that the female lays the egg in late May or June. The captive Emperors laid their eggs in mid- to late July. This could be due to the birds' lack of experience or to the lighting schedule.

Prevost (1953) noted that most eggs are laid between 0200 and 0700 hours. I saw one egg being laid, at 1103 hours. Since the other eggs were all discovered between 0740 and 1154 hours, I assume they were laid in the morning (Table 1).

Prevost (1953) stated that contractions during egg-laying occur every two minutes, with the pointed end of the egg emerging first and the female being very irritable. #11Y seemed to have much more closely spaced contractions, but the episode agreed with Prevost's description in all other respects.

Egg Exchanges

The exchanges I observed agree with descriptions by Stonehouse (1953), who suggested that the female's action of turning around before giving up the egg serves to pack down the snow and provide a smooth surface for the exchange.

The pattern of the exchanges also followed that described by Prevost (1953). The pairs became active, vocalizing frequently. The female began showing the egg to her mate, and both began touching the egg with their beaks. Each partner initiated the trumpet display and their partners responded.

After giving the egg to the male, the female stayed next to him for a few minutes, vocalizing and showing her brood patch, then walked around the unit, followed by the male.

Incubation

Emperor Penguins have an incubation period of 62 to 64 days (Prevost, 1961). This coincides with the female's first feeding period at sea, an absence of 60 to 70 days (Prevost, 1961). The length of the incubation periods that I observed was 64 ± 4 days (range = 58-66), slightly longer than Prevost's 62 to 64 days.

Broodiness in birds is stimulated by prolactin secretion, and it has been suggested that even non-breeding Emperors produce enough prolactin to cause broodiness, providing additional birds to incubate abandoned eggs or chicks (Murphy, 1936). The captive birds expressed no interest in the eggs although the general activity level in the unit increased on days when eggs were laid. In 1979 the staff observed a "scrimmage" in which non-breeders attempted to take an egg (Todd, 1980).

There is much individual variation in interest in incubation. Prevost (1953) wrote of three classes of incubating Emperors: timid (those which abandon their egg readily), normal, and aggressive (those which defend their egg from neighbors and search for a lost egg). I observed a similar variation. One egg was abandoned within 24 hours of discovery, while another pair incubated a dummy egg for the entire incubation period (61 to 68 days).

After egg-laying, the female's motivation to incubate decreases until she gives the egg to the male, whose desire to incubate is increasing (Stonehouse, 1953). The incubating bird is usually reluctant to give up an egg or chick and may even try to take it back from its mate if the mate appears to be having trouble holding it (Stonehouse, 1953). This reluctance was demonstrated by one of the pairs I studied. The female placed the egg on the ice eight times, but picked it up herself each time. When the egg was removed, she readily accepted a dummy egg, which she incubated for 78 hours before giving it to the male.

Eggless birds are much more active than their incubating counterparts, who tend to huddle and remain still (Stonehouse, 1953). The birds with eggs that I observed were inactive, preening occasionally and rarely moving around the enclosure.

There has been some disagreement as to whether or not Emperors will incubate only their own eggs. Murphy (1936) stated that many birds took turns incubating chicks and eggs. Prevost (1953) wrote that the egg is only brooded by the parent and only the mate will relieve it. In some cases, however, an abandoned egg will be adopted (Prevost, 1953).

Emperors do not appear to recognize their eggs, which lack any distinctive markings, and will accept dummy eggs. Prevost (1958) found that a bird presented with its own egg and another egg will take either the closer egg or the egg seen first, whether or not the egg is its own.

Eggs may be abandoned for a variety of reasons. It the mate does not return to relieve an incubating bird in time, it may be forced to abandon the egg and go to sea to feed. Eggs may also be abandoned earlier in the incubation period by inexperienced birds (Prevost, 1969). The birds I studied were inexperienced; the eggs laid in 1980 were the second set of eggs (the first to hatch). Of the two eggs laid the previous year (1979), one was left on the ice so often it was replaced with a dummy, which was also abandoned. The second egg was found in a pool, as was the dummy that replaced it (Todd, 1980). One of the 1980 eggs was also lost in a pool. Since none of the birds looked too thin, I attributed the abandonments to inexperience rather than to hunger.

Infertile eggs are generally abandoned several days after their expected hatching date. There are records of birds incubating the dummy egg until the expected hatching date and then abandoning it.

Once they begin incubating, the males form huddles in the wild (Prevost, 1953). Stonehouse (1953) found no affinity towards pairing among incubating birds. However, Mougin (1966) found that two or three

males might stay together, pecking at neighbors and vocalizing to each other. Although the incubating birds I studied were all kept in an enclosure they did not huddle, probably because the temperature was not as extreme as it would have been in the wild. The incubating males did not have any special attraction or groups, but stayed with their mates whenever the mate was in the enclosure.

Chicks

I observed the chicks from hatching to 10 days old (Table 1). They were covered with light gray down on their bodies and black and white down on their heads. The fine down allows the heat of the parent's body to be transferred easily to the chick, which cannot thermoregulate until it is about 20 days old (Prevost, 1961). To minimize disturbance, we did not weigh or measure the chicks.

The parents held the chicks on their feet, putting them back immediately if they fell off. According to LeMaho (1977), the chicks remain on the adult's feet until they are about a month old. Then they form groups called creches (Sparks and Soper, 1967).

The chick is usually fed first by the mother, who returns from feeding at sea about the time hatching begins. The female broods and feeds the chick for approximately four weeks while the male is at sea (LeMaho, 1977). If the female is late returning, the male can feed the chick with a secretion similar to pigeons' crop milk (Prevost, 1961).

After hatching, the chick is fed almost hourly with regurgitated stomach contents. The feeding soon decreases to two or three daily (Prevost, 1961). My observations showed a similar schedule of feedings for the chicks. The regurgitation is stimulated by vocalizations and movements of the chick (Stonehouse, 1953).

My observations showed that feeding was stimulated by movements and vocalizations of the chicks and also by another bird feeding its

chick. As the chick started to move the parent would lift its brood patch several times, and the chick would begin vocalizing. The adult would regurgitate, bend over and open its beak so that the chick could feed. Three times I observed mates who were not holding their chicks begin to regurgitate when the chicks started to vocalize.

There is some debate as to whether or not adults recognize and feed only their own chicks (Prevost, 1961; Murphy, 1936). The chicks I studied were fed only by their own parents. Finding mates was much easier for the captive birds than for birds in the wild, where breeding colonies are much larger. The captive birds had only to find their mate and they would then feed their own chicks. Adults may recognize the vocalizations of their chicks, but my data are insufficient to confirm this theory.

Pair Bonding

In Emperor Penguins the formation of a strong bond that lasts throughout the breeding season is necessary for reproductive success. The male and female must coordinate feeding trips to the ocean and incubation duties in order to raise a chick.

Lack (1940) described five types of pair bonding in birds. These are: (1) for copulation only, (2) for a few days, (3) for a time after copulation, (4) for one breeding season, (5) for life.

Most marine birds form pairs for breeding and establish territories (Etkin, 1964). Courtship behaviors may persist after pair formation in the form of elaborate greeting or nest relief ceremonies (Smith, 1977). Burton (1953) has also noted that courtship behavior often appears out of breeding season in bird species that are monogamous.

In most penguin species the pair bond appears to last through several seasons, although species as well as individual variation has been observed (Richdale, 1951). In Adelies, 83% of the pairs studied

reunited the following year, while in Yellow-eyed Penguins 39% of the bonds lasted 2 to 6 years, and 3% lasted 7 to 13 years (Sparks and Soper, 1967). Observations on captive King Penguins showed that they tended to stay with one mate for several years (Richdale, 1951).

For Emperor Penguins the problem of finding the previous year's mate is compounded by the huge breeding colonies and the lack of an established territory on which a pair can meet. The tendency of some birds to reunite with their mate may be due to the fact that they both have returned to their nesting territory (Lack, 1940).

Studies on Emperors have shown that fidelity during a particular season is high, but year to year fidelity is low. During one season Prevost (1961) tagged 73 pairs, 54 of which stayed together throughout the breeding season. When separated these birds searched actively for their mates. Jouventin (1971b) banded and separated 54 pairs and found that 50 (92.6%) of them reunited. Although I had a much smaller sample, the birds I studied also searched actively for their mates and returned to their mates whenever possible.

In terms of year to year fidelity, Isenmann (1971) found that only 6 of 41 banded pairs reunited the following year. Jouventin (1971b) also noted that year to year fidelity was low, although several 3 or 4 year bonds were noted.

Trumpet Display

In the trumpet display the bird bends over, takes a deep breath, and begins the call while raising the head, ending with the head held upright. The male and female have slightly different ending notes in this display, the male's final note being longer (Scheich, 1980). This display has also been described by Stonehouse (1953) and Prevost (1961).

Stonehouse (1953) theorized that the trumpet display is a relic from the time when Emperors were territorial, as the closely related

King Penguins are. More elaborate displays, such as those seen in other penguins, that reduce aggression and allow colonial breeding, may have been lost or deteriorated in the Emperor to the present behavior.

Jouventin (1971a) suggested that the trumpet display functions in sexual identification. This seems plausible, as with practice a human observer can learn to distinguish by ear between the male and female calls (Prevost, 1961). Scheich (1980) worked with captive birds and confirmed the two distinct calls, naming them the M-type and the F-type. In the present study Bowles and I obtained 83% agreement between call type and sex determined by copulation attempts and incubation roles (Table 2).

It has been suggested that individual variation in the trumpet display allows individual recognition between Emperors (Jouventin, 1971b). Prevost (1961) agrees that this is a possibility, but he did not confirm the theory by experiments. Scheich (1980) concluded that the calls did allow individual recognition. He played three calls: a "foreign" call recorded in Antarctica and presumably never heard by the captive birds, a synthetic call, and a familiar call. The response was greatest to the foreign call, less to the synthetic call, and least to the familiar call. Whether this demonstrates recognition or simply a response to a novel situation is not clear.

Although I noted the trumpet display by non-breeding birds throughout the season, the breeding birds did not trumpet during the 2 to 4 weeks of observation prior to egg-laying. Jouventin (1971a) also observed this prepositial silence.

Sideways Stare

In the sideways stare the two birds stand close together, lean apart, and stand motionless. The birds seem to have a decreases awareness of their surroundings and can be approached easily during this display (Prevost, 1961).

This display is often preceded by the trumpet display. It is almost always followed by head shakes or swallowing movements. Isenmann (1971) also observed the display walk after the sideways stare, as my studies confirmed.

The sideways stare has been noted between non-breeding birds, between mates when one is returning from an absence, and between males and females of different pairs with eggs (Prevost, 1961). Its function appears to be similar to that of the mutual display of Adelie Penguins, i.e., visual recognition and maintenance of the pair bond (Prevost, 1961).

Head Movements

I observed 3 head movements. The first was horizontal shaking, which occurred after the trumpet display, sideways stare, or by itself. When this movement appeared alone, it seemed to be simply a comfort movement. The penguin is usually standing in a relaxed posture with its head and neck low. The shaking may serve to remove salt from the ends of the supraorbital glands (Ainley, 1974), or simply to stretch the neck after periods of inactivity.

When performed after the trumpet display or sideways stare, the function of the head shake may be to show the colorful ear patches, as the similar "head-flagging" does in Royal Penguins (Isemann, 1971). It may also interrupt the visual interaction of the preceding display. Chance (1962) states that head turning is gulls may function in this manner, lessening the likelihood of actual aggression aroused by mutual gazing. Since both the trumpet and the sideways stare involve mutual gazing, the head shake could be important in reducing aggression, allowing the birds to give up any personal space and huddle together for protection against the weather.

The second movement is the head twist, which is also performed after aggressive lunges or trumpet displays. It may serve a similar function in reducing aggression.

The third movement is the head nod, in which the head is moved up and down, and which may be accompanied by swallowing movements. Prevost (1961) noted this movement after displays and aggressive interactions. I observed it in the same situations and also after comfort movements such as stretching and preening.

Display Walk

Although Jouventin (1971b) states that the Emperors have lost the "swinging" or display walk seen in King Penguins, Prevost (1961) did observe it. I observed the captive birds performing the display walk twice.

The King Penguins' display walk is supposed to attract females to the male's territory (Jouventin, 1971b). Sparks and Soper (1967) state that the walk may help display the Kings' colorful ear patches, which Emperors also have.

It is possible that the captive Emperors learned the display walk from the Kings in the unit. However, this does not seem likely.

Single Note Cry

The single note cry, also called the trumpet cry by Jouventin (1971a), allows separated birds to regroup (Jouventin, 1971a). My observations support this, since I noted it only when a pair was separated, either by myself or by the wall of the enclosure.

Conclusion

While the study of captive birds cannot replace observations of birds in the wild, it does allow more detailed studies of individuals in a controlled environment.

Several deviations from the breeding cycle reported by other researchers were noted. These included less huddling by Emperors and no huddles formed by incubating birds. Since huddles are important in thermoregulation, the higher temperatures the captive birds were exposed to (as opposed to temperatures in the wild) can account for this change in behavior. The number of birds (much smaller than in a natural breeding colony) may also have affected huddling. It is interesting that non-breeding birds still huddle occasionally, even though the temperature is not extreme, but breeding birds do not huddle at all under the favorable conditions in the unit.

Deviations from the austral lighting schedule at Sea World may account for the lateness of the breeding cycle. The lack of a seasonal temperature change may also have played a role in the delayed cycle.

The egg-laying contractions observed in this study were much more closely spaced than those reported by Prevost (1961).

Lack of experience may account for several variations in exchanges of eggs and incubation periods. The exchanges took longer than those reported by other researchers. During incubation, an egg was abandoned by a bird that had not lost a great deal of weight. I believe that the abandonment was brought about by the bird's lack of experience.

Inexperience does not account for the incubation time, which was longer than that reported by other observers. Perhaps the change in environment or the small sample size can account for this.

While studying chicks I found that feeding was stimulated by the chicks' restlessness and vocalizations. I also observed that some parents were stimulated to regurgitate even when they were not

holding their chicks. Parents were also stimulated to feed when birds around then began feeding their chicks.

The pair bond is very important to Emperors in the wild which must cooperate with their mates in order to successfully raise a chick. I found the seasonal pair bond was very strong; even though allowed to leave the enclosure, the birds consistently returned to their incubating mates.

My observations of the trumpet display confirmed other researchers' hypothesis (Jouventin, 1971a; Prevost, 1961) that it is important in sexual identification; however, they neither support nor disprove the theory that the trumpet display allows individual identification (Jouventin, 1971b; Scheich, 1980). Similarly, the sideways stare facilitates sexual identification.

The display walk of the King Penguin, described by Jouventin (1971a), was observed in captive Emperor Penguins. Whether Jouventin simply did not observe this display in Emperors, or the Emperors learned it from the King Penguins in the unit is not clear from my data.

The single note cry I observed allowed the separated birds of a pair to find each other, as proposed by Jouventin (1971a).

Sexing by vocalization done by Bowles and myself was confirmed in 10 out of 12 birds (83%) by egg-laying and/or incubation roles. In the two cases (a pair of birds) that did not conform, I found that the female (according to vocalization) assumed incubation duties that are usually performed by the male. I attribute this to the birds' lack of experience in breeding and to the accessibility of food. In the wild the female would have had to leave the egg with the male in order to feed at sea. I believe that the sexing by vocalization of these two birds was also correct.

The observations of captive birds confirmed the hypotheses of previous researchers. The only major differences can be attributed (for the most part) to changes in lighting and temperature, which help to determine how these factors affect the behavior of Emperor Penguins in the wild.

The Sea World facility has the potential for many more studies of penguin behavior, growth, and physiology. The hatching of chicks for the first time in captivity will provide opportunities to obtain much needed information on growth, development, and ontogeny of behavior patterns.

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Table 1. 1980 Breeding Season: Emperor Penguin Egg Data.

Pair		date egg laid	time egg found	time of egg exchange	final outcome
24Y	40Y	11 July	0840	1303	lost in pool
13G	1G	11 July	1154	not completed	infertile
27Y	4G	12 July	0748	not known	hatched 16 Sept.
17Y	6Y	17 July	1034	1145	hatched 21 Sept.
11Y	3Y	17 July	1103	not known	hatched 21 Sept.
UM	6G	28 July	not known	not known	hatched 24 Sept.

Table 2. Sexual Identification of Breeding Emperor Penguins.

Penguin	Copulation Role	Egg-laying	Incubation Role	Vocalization
3Y	Male	...	Male	Male
24Y	Female	...	Female	Female
40Y	Male	...	Male	Male
1G	Male	...	Male	Male
13G	Female	...	Female	Female
17Y	Female	...	Female	Female
6Y	Male	...	Male	Male
11Y	Female	Female	Female	Female
6G	...	...	Male	Male
UM	...	...	Female	Female
4G	...	...	Male	Female
27Y	...	...	Female	Male

Table 3. Sexes of Displaying Emperor Penguins: Trumpet and Sideways Stare Displays.

	between males	between females	between male and female
Trumpet Display	7	3	41
Sideways Stare Display	0	3	12

Table 4. Analysis of Sideways Stare Display of Emperor Penguins.

When Display Observed	Number of Times	% of Total
Sideways stare alone	31	45.0
After trumpet display	29	42.0
Before trumpet display	6	8.5
After copulation	1	1.5
Before display walk	1	1.5
After display walk	1	1.5

Table 5. Analysis of Head Movements of the Emperor Penguin.

	nod	twist	shake
After copulation attempt	1	3	0
After pair separated	4	0	1
Disturbed by other bird	2	4	0
After trumpet display (not completed)	6	2	0
Before sideways stare	2	2	0
After sideways stare	4	2	0
After pointing to own or mate's brood patch	7	3	0
After showing chick	12	1	1
During comfort behavior	4	0	6

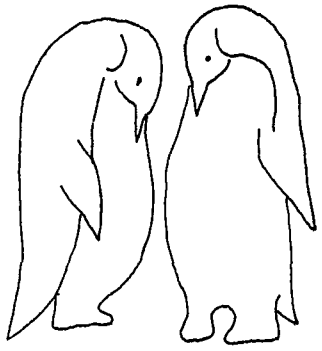

Figure 1. Trumpet Display of Emperor Penguin.

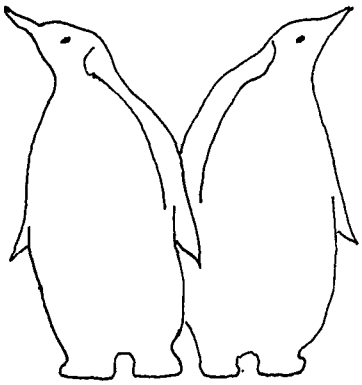

Figure 2. Sideways Stare Display of Emperor Penguin.